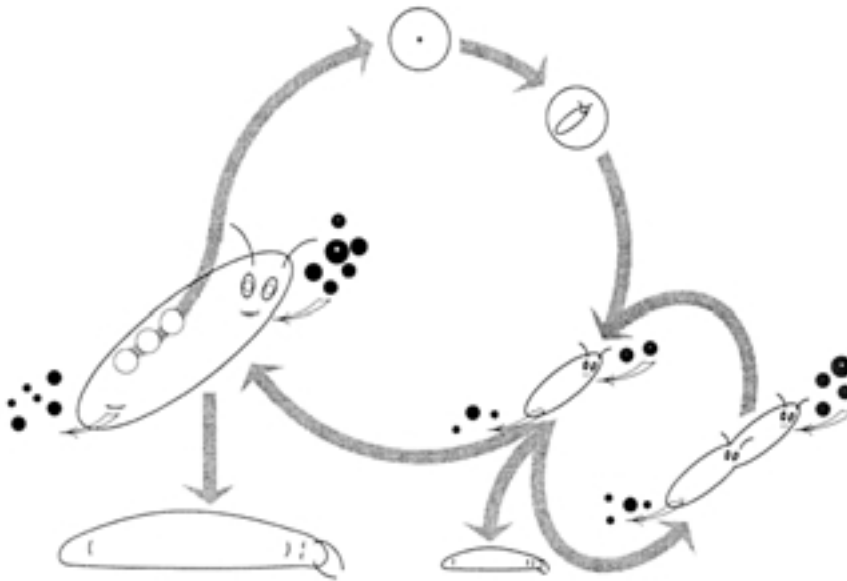


Second Edition

Dynamic Energy and Mass Budgets in Biological Systems

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Contents

Preface to the second edition	xi
Preface	xiii
Book organization	xvi
Acknowledgements	xviii
1 Energetics and models	1
1.1 Energy and mass fluxes	1
1.1.1 Hope for generality	1
1.1.2 Historical setting	3
1.1.3 Energetics	5
1.1.4 Population energetics	6
1.2 The art of modelling	7
1.2.1 Strategies	7
1.2.2 Systems	11
1.2.3 Physical dimensions	12
1.2.4 Statistics and support	14
1.3 Summary	17
2 Basic concepts	19
2.1 Individuals: the basic level of organization	19
2.1.1 Input/output relationships	19
2.1.2 State variables	20
2.2 Body shape: surface area/ volume relationships	23
2.2.1 Isomorphism	25
2.2.2 Changing shapes	26
2.3 Body size and composition	30
2.3.1 Homeostasis	30
2.3.2 Weights	31
2.3.3 Masses	33
2.3.4 Biomass composition	34
2.3.5 Energy	35
2.3.6 Storage materials	37
2.4 Concentrations, amounts and fluxes	40

2.4.1	Enzyme kinetics	41
2.4.2	Synthesizing Units	43
2.4.3	Production of generalized compounds	48
2.4.4	Handshaking protocols	48
2.5	Metabolic modes	51
2.6	Temperature	53
2.7	Life-stages	59
2.8	Summary	63
3	Energy acquisition and use	65
3.1	Feeding	66
3.1.1	Feeding methods	66
3.1.2	Feeding and movement costs	71
3.1.3	Functional response	73
3.1.4	Diet	76
3.1.5	Food deposits and claims	78
3.2	Digestion	79
3.2.1	Smoothing and satiation	79
3.2.2	Gut residence time	81
3.3	Assimilation	81
3.4	Reserve dynamics	82
3.5	The κ -rule for allocation	86
3.6	Maintenance	89
3.6.1	Volume-related maintenance costs	90
3.6.2	Surface-area-related maintenance costs	91
3.7	Growth	94
3.7.1	Embryonic growth	96
3.7.2	Growth for non-isomorphs	108
3.8	Development	111
3.9	Propagation	113
3.9.1	Reproduction	114
3.9.2	Division	118
3.10	Summary of the basic DEB model	120
4	Uptake and use of essential compounds	125
4.1	Chemical compounds and transformations	125
4.2	Powers	129
4.3	Mass balance	130
4.3.1	Partitioning of mass fluxes	131
4.3.2	State versus flux	133
4.3.3	Mass investment in neonates	133
4.3.4	Composition of reserves and structural mass	134
4.4	Respiration	135
4.4.1	Respiration Quotient	137

4.4.2	Heat increment of feeding	138
4.4.3	Aging as a consequence of respiration	139
4.5	Nitrogen balance	145
4.5.1	Urination Quotient	146
4.5.2	Ammonia excretion	147
4.6	Products	147
4.7	Fermentation	148
4.8	Water balance	151
4.8.1	Doubly labelled water	152
4.8.2	Plant-water relationships	152
4.9	Energy balance	153
4.9.1	Dissipating heat	153
4.9.2	Indirect calorimetry	155
4.9.3	Thermodynamic constraints	155
4.10	Summary	156
5	Multivariate DEB models	159
5.1	Several substrates	160
5.1.1	Substitutable substrates	160
5.1.2	Supplementary substrates	164
5.1.3	Photosynthesis <i>sensu lato</i>	164
5.1.4	Calcification	167
5.2	Several reserves	168
5.2.1	Growth	168
5.2.2	Reserve dynamics	170
5.2.3	Simultaneous nutrient limitation	171
5.2.4	Non-limiting reserves can dam up	172
5.2.5	Oxygen flux	174
5.2.6	Ammonia-nitrate interactions	175
5.3	Several structural masses	177
5.3.1	Organ size and function	179
5.3.2	Roots and shoots	179
5.4	Summary	184
6	Uptake and effects of non-essential compounds	187
6.1	One-compartment kinetics	189
6.2	Partition coefficient	191
6.2.1	Kinetics as a function of partition	191
6.2.2	Kinetics as a function of ionization	193
6.3	Energetics affects toxicokinetics	195
6.3.1	Dilution by growth	195
6.3.2	Changes in lipid content	196
6.3.3	Bioconcentration coefficient	199
6.3.4	Metabolic transformations	201

6.4	Toxicants affect energetics	202
6.4.1	No effects	204
6.4.2	Effects on survival	205
6.4.3	Effects on growth and reproduction	209
6.4.4	Receptor-mediated effects	213
6.4.5	Mutagenic effects	214
6.4.6	Effects of mixtures	217
6.4.7	Population consequences of effects	217
6.5	Summary	219
7	Case studies	221
7.1	Changing feeding conditions	221
7.1.1	Scatter structure of weight data	221
7.1.2	Step up/down in food availability	223
7.1.3	Mild starvation	223
7.1.4	Food intake reconstruction	223
7.1.5	Prolonged starvation	227
7.1.6	Shrinking	230
7.1.7	Dormancy	231
7.1.8	Emergency reproduction	232
7.1.9	Geographical size variations	232
7.2	Diffusion limitation	235
7.2.1	Homogeneous mantle	235
7.2.2	Mantle with barrier	238
7.2.3	Non-homogeneous mantle	238
7.3	Digestion	239
7.3.1	Comparison of substrates	241
7.4	Cell wall and membrane synthesis	243
7.5	Protein synthesis	244
7.6	Structural homeostasis	246
7.7	Growth of dynamic mixtures of morphs	250
7.7.1	Crusts	250
7.7.2	Flocs and tumours	251
7.7.3	Roots and shoots	252
7.8	Pupa and imago	253
7.9	Changing parameter values	257
7.9.1	Changes due to body temperature	258
7.9.2	Changes at puberty	260
7.9.3	Changes in response to the photoperiod	262
7.9.4	Suicide reproduction	262
7.9.5	Adaptation	263
7.10	Summary	264

8	Comparison of species	265
8.1	Genetics and parameter variation	265
8.2	Body size scaling relationships	267
8.2.1	Primary scaling relationships	268
8.2.2	Secondary scaling relationships	270
8.2.3	Tertiary scaling relationships	289
8.3	Allocation strategies	290
8.3.1	r versus K strategy	290
8.3.2	Small versus large eggs	291
8.3.3	Egg versus foetus	292
8.3.4	Versatility versus specialization	292
8.3.5	Growth versus reproduction: determinate growth	293
8.4	Evolutionary aspects	298
8.5	Summary	300
9	Living together	301
9.1	Trophic interactions	301
9.1.1	Competition	301
9.1.2	Syntrophy	302
9.1.3	Symbiosis	304
9.1.4	Biotrophy and parasitism	309
9.1.5	Predation and saprotrophy	309
9.2	Population dynamics	310
9.2.1	Non-structured populations	312
9.2.2	Structured populations	320
9.2.3	Mass transformation in populations	335
9.3	Food chains and webs	342
9.3.1	Transient behaviour of bi-trophic chains	342
9.3.2	Asymptotic behaviour: bifurcation analysis	344
9.4	Canonical community	350
9.4.1	Mass transformations in communities	352
9.5	Summary	355
10	Evaluation	357
10.1	Energetics and metabolism	357
10.2	Principles of the DEB theory	358
10.3	Other approaches	363
10.3.1	Static Energy Budgets	363
10.3.2	Net production models	365
	Bibliography	367
	Glossary	401
	Notation and symbols	407

Taxonomic index	415
Subject index	419

Chapter 1

Energetics and models

This introductory chapter presents some general background to theoretical work in energetics. I start with an observation that feeds the hope that it is possible to have a theory that is not species-specific, something that is by no means obvious in view of the diversity of life! A brief historical setting follows giving the roots of some general concepts that are basic to Dynamic Energy Budget (DEB) theory. I will try to explain why the application of allometry restricts the usefulness of almost all existing theories on energetics. This explanation is embedded in considerations concerning philosophy and modelling strategy to give the context of the DEB theory.

1.1 Energy and mass fluxes

1.1.1 Hope for generality

Growth curves are relatively easy to produce, which may explain why the literature is full of them. Yet they remain fascinating. When environmental conditions, including temperature and food availability, are constant and the diet is adequate, organisms ranging from yeasts to vertebrates follow, with astonishing accuracy, the same growth pattern as that illustrated in Figure 1.1. This is amazing because different species have totally different systems for regulating growth. Some species, such as daphnids, start to invest, at a certain moment during growth, a considerable amount of energy in reproduction. Even this does not seem to affect their growth curve. So one wonders how the results can be so similar time and again. Is it all a coincidence, resulting from a variety of different causes, or do species have something in common despite their differences? Are these curves really similar, or is the resemblance a superficial one?

Some workers do not believe that the growth of animals, plants and other organisms can be captured in a single framework. Many concepts, such as the decomposition of mass into a storage and structural component and uptake across surface areas, are standard elements of plant production modelling [671], and equally apply to animals and micro-organisms. Thornley [921] presented arguments against a single framework. One of them is that growth is confined to specialised tissues (meristems) in plants, but this is not dissimilar to growth of the tips of fungal hyphae, or of bacterial cells for instance. Another is that

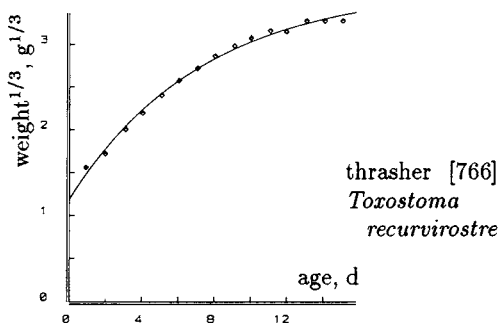
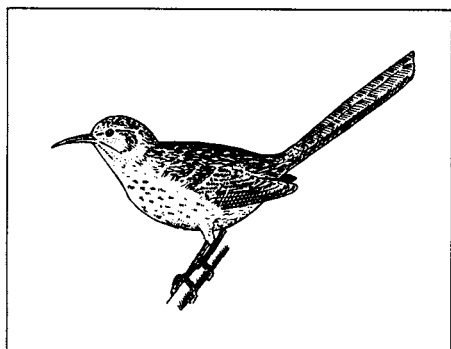
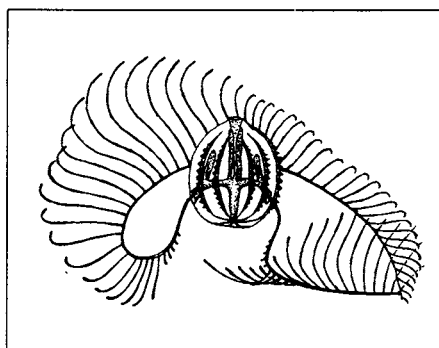
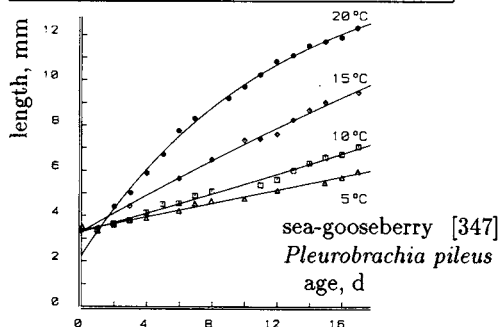
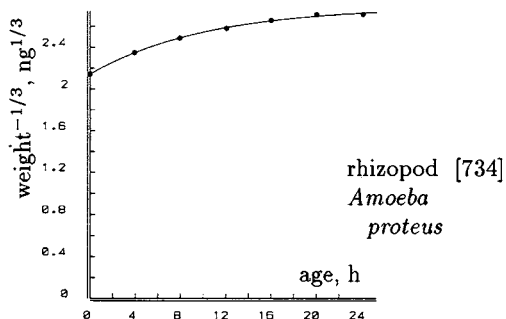
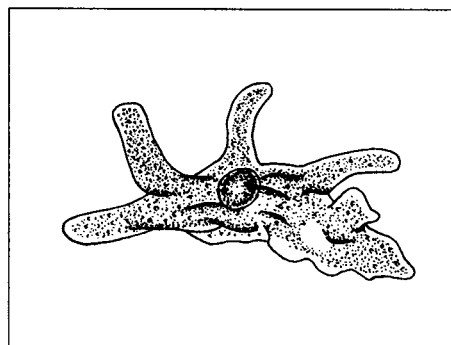
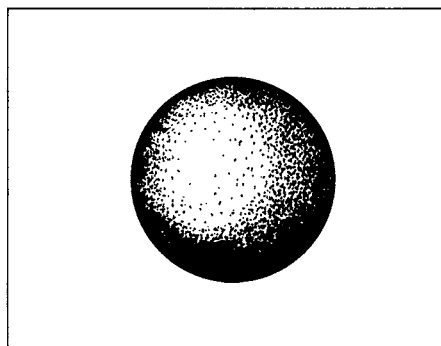
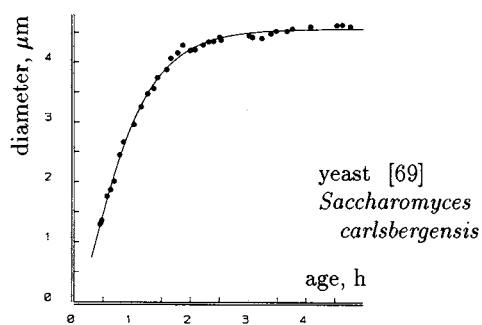


Figure 1.1: These growth curves all have the shape $L(t) = L_{\infty} - (L_{\infty} - L_0) \exp\{-\dot{r}_B t\}$, while the organisms differ considerably in their growth-regulating systems. How is this possible? Data sources are indicated by entry numbers in the bibliography.)

growth is frequently indeterminate in plants, and determinate in animals. However, the wide applicability of von Bertalanffy's growth curve for animals shows that the latter is not generally true, while determinate growth can also be understood in the context of a single general framework, see {293}.

My attempts to understand similarities in growth curves led me on a breathtaking hike into many corners of biological territory. They became an entertaining puzzle: is it possible to construct a set of simple rules, based on mechanisms for the uptake and use of material by individuals, that is consistent with what has been measured? The early writers made a most useful start: growth results from processes of build-up and break-down. Break-down has something to do with making energy and elementary compounds available, so how are they replenished? What processes determine digestion and feeding? What determines food availability? Build-up results in size increase, and so affects feeding, but offspring are produced as well. This obviously affects food availability. Where does maintenance fit in? Why should there be any maintenance at all? What is the role of age? These are just some of the questions that should be addressed to satisfactorily explain of a growth curve.

The comparison of different systems that share common principles can be a most powerful tool in biology. I give two examples, which are discussed later {95,103}.

Individuals of some species, such as humans, lose their ability to grow. Cartilage tissue is replaced by bone, which makes further growth impossible. Is this why growth stops? This question cannot be answered by studying these species, because they stop growing and also change cartilage to bone. The answer should be 'no', I think, because it is possible to formulate a model for growth that applies to these species as well as to those that continue to grow, such as fish. Growth in mammals would cease even if they did not lose their ability to grow, and cartilage is replaced, possibly to obtain a mechanically better structure.

Another example is the egg shell of birds, which limits the diffusion of oxygen and, therefore, the development of the embryo, according to some authors [747]. A frequently used argument is the strong negative correlation between diffusion rates across the egg shell and diffusion resistance, when different egg sizes are compared, ranging from hummingbirds to ostriches; the product of diffusion rate and resistance does not vary a lot. Again I think that the shell does not limit the development of the embryo, because it is possible to formulate a model for embryo development that applies to birds as well as to animals without rigid egg shells. The physical properties of the egg shell are well adapted to the needs of the embryo, which causes the observed correlation.

The crux of the argument is that the same model applies to different systems and that the systems can be compared on the basis of their parameters.

1.1.2 Historical setting

Many of these questions are far from new. R. Boyle, R. Hooke and J. Mayow in the seventeenth-century were among the first to relate respiration to combustion, according to McNab [615]. The first measurements of the rate of animal heat production were made by A. Crawford in 1779, and A. L. Lavoisier and P. S. de Laplace in 1780 aimed to relate it to oxygen consumption and carbon dioxide production [615]. Interest in how metabolic rate, measured as oxygen consumption rate, depends on body size goes back at least as

far as the work of Sarrus and Rameaux [807] in 1839. They were the first to find rates proportional to surface area for warm-blooded animals [79]. Later this became known as the Rubner's surface law [794]. Pütter [741] used it in a model of the growth of individuals in 1920. He saw growth as the difference between build-up and break-down. The processes of build-up, which later became known as anabolic processes, were linked directly to the metabolic rate, which was assumed to follow the surface law. The processes of break-down, now known as catabolic processes, were assumed to proceed at a constant rate per unit of volume. Volume was thought to be proportional to weight. The growth rate then results from a weighted difference between surface area and volume. The casual way A. R. Wallace mentioned this idea in a note to E. B. Poulton (appendix 3 in [281]) suggests that its roots go back to before 1865. The resulting growth curve is presented in Figure 1.1. The fact that Pütter applied the model to fish, whereas the surface law was based on work with warm-blooded animals, generated a lot of criticism.

More data were generated with improved methods of measurement; invertebrates were also covered. Kleiber [491] found in 1932 that metabolic rates are proportional to weight to the power 0.75 and this became known as Kleiber's law. Extensive studies undertaken by Brody [119] confirmed this proportionality. Von Bertalanffy [79] saw anabolic and catabolic rates as special cases of the allometric relationship, i.e. a relationship of the type $y = \alpha x^\beta$, where y is a variable dependent on another variable x , usually body weight. He viewed this as a simplified approximation that could be applied to almost all types of metabolic rates, including the anabolic and the catabolic, but the constant β varies somewhat with the tissue, physiological conditions and experimental procedure. The growth curve proved to be rather insensitive to changes in β for catabolism, so, like Pütter, von Bertalanffy took the value one and classified species on the basis of the value for β of anabolism. The surface law is just one of the possibilities.

Although von Bertalanffy [78] was the genius behind the ideas of general systems theory, he never included the feeding process in his ideas about growth. I do not know why, because mass balance equations are now always bracketed together with systems. I think that the use of allometric equations, which is a step away from mechanistic explanations towards meaningless empirical regressions, obstructs new ideas in metabolic control. I will explain this in later sections. The idea of allometry goes back to Snell [866] in 1891 and, following the work of Huxley [438], it became widely known. Both Huxley and von Bertalanffy were well aware of the problems connected with allometric equations, and used them as first approximations. Now, a century later, it is hard to find a study that involves body size and does not use them.

Zeuthen [1027] was the first to point to the necessity of distinguishing between size differences within a species and between species. The differences in body size within a species, as measured in one individual at different points during development, are treated here as an integral part of the processes of growth and development. Those between species are discussed in a separate chapter on parameter values {comp}, in which I show that body size scaling relationships can be deduced without any empirical arguments.

1.1.3 Energetics

The problem that everything depends on everything else is a hard one in biology, as anything left out may prove to be essential in the end. If one includes as much as possible one loses an intellectual grasp of the problem. The art is to leave out as much as possible whilst maintaining the essence. I focus the discussion on an abstract quantity, called energy, rather than a selection of the many thousands of possible compounds usually found in organisms. No selection can be inclusive, so what is the role of compounds that are left out? Jeong *et al.* [450] made a heroic attempt to model the compound-based physiology of *Bacillus* and introduced more than 200 parameters. However, many compounds have yet to be identified and the quantities and dynamics of most compounds are largely unknown. Moreover, the main components of organisms such as yeasts and vertebrates are different. So investigating compounds does not seem a promising route to understand the similarity in growth curves.

A better route would be to use the concept of energy, meaning something like ‘the ability to do work’, which primarily consists of driving chemical reactions against the direction of their thermodynamic decay. The term was first proposed by Thomas T. Young in 1807, according to Blaxter [92]. Energy is stored in a collection of (organic) compounds, so a full explanation requires the inclusion of mass fluxes, as I will explain on {35}. It is important to realize here that there is a close link between energy and mass flows.

Proteins in food are first decomposed into amino acids, and amino acids are polymerized to proteins again. A similar process applies to carbohydrates and lipids, which together with proteins constitute the main materials of life. The decomposition of many types of source materials into a limited number of types of central metabolites before polymerization into biomass is known as the ‘funnel’ concept. The rich diversity of catabolic machinery, especially among the prokaryotes, and the poor diversity of anabolic machinery was recognized by Kluver and Donker in 1926 [494].

The role of energy in cellular metabolism, in particular the generation and use of ATP, is the main focus of bioenergetics [646]. This compound is called the energy currency of the cell. Together with NADPH and NADH, which provide reducing power, it drives the anabolic processes. Compounds involved in the decomposition processes are important for the cell in two ways: through the production of ATP from ADP and P, which is produced in anabolic processes, and through the production of elementary compounds that are substrates for anabolic processes [416]. The final stages of the catabolic processing of lipids, carbohydrates and proteins all make use of the same cellular machinery: the Krebs cycle. To some extent, these substrates can substitute each other for fuelling purposes. The cell chooses between the different substrates on the basis of their availability and its need for particular substrates in anabolic processes.

After this introduction, it perhaps comes as a surprise that ATP is not the main focus in eco-energetics. This is because ATP itself does not play a leading role in energy fluxes. It has a role similar to that of money in your purse, while your bank account determines your financial status. A typical bacterial cell has about 5×10^6 ATP molecules, which is just enough for 2 seconds of biosynthetic work [551]. The mean lifetime of an ATP molecule is about 0.3 seconds [370]. The cell has to make sure that the adenylate energy

charge ($\frac{1}{2} \text{ ADP} + \text{ATP}$) ($\text{AMP} + \text{ADP} + \text{ATP}$)⁻¹ remains fairly constant (usually around 0.9, but this matter is not settled yet). It does so by coupling endergonic (energy requiring) and exergonic (energy releasing) reactions. If the energy charge is reduced, the energy yield of the reaction $\text{ATP} \rightarrow \text{ADP} + \text{P}$ declines rapidly. The situation where the energy charge as well as the concentration of $\text{AMP} + \text{ADP} + \text{ATP}$ remain constant relates to the concept of homeostasis, {30}. Cells keep their purses well filled, which makes the dynamics of the purse contents less interesting. ATP is part of the machinery used to harvest or mobilize energy.

A varying energy yield per mole of ATP does not necessarily complicate metabolic dynamics. It primarily affects the rate at which ATP is produced in energy-yielding transformations or consumed in energy-requiring transformations, and therefore also the rate at which ATP and ADP commute between the sites where these transformations occur. The analogy with money can be extended one step further: the big bank-money is in a stable currency, while the exchange rate of the small purse-money may vary. The focus on ATP/ADP versus polymers is primarily a question of relevant time scales. Cell division cycles and stages in the development of individuals last too long for a focus on ATP.

The chemiosmotic theory was developed to explain the molecular mechanism of ATP generation. It has boosted biochemical research in cellular energetics, and it is now a central issue in all texts on molecular biology [664], although competing theories do exist [562]. The focus of bioenergetics on the processes of ATP synthesis and use matches the classic division of metabolism into catabolic and anabolic processes very well [988]. This division, however, is less straightforward in the context of the DEB theory, where reserves play an essential role, and processes of synthesis and decomposition occur repeatedly in metabolism. Other differences exist as well. Cell size influences cellular processes through the ratio between membrane surface area to cell volume. This gives the DEB theory a natural focus on cell and life cycles. The link between activity coupled to a surface area (membrane) and mass of metabolic substrate and product coupled to volume is a cornerstone in the DEB theory for the uptake and use of energy.

1.1.4 Population energetics

If a population consists of individuals who take up and use energy in a particular way, how will it behave in a given environment? If populations are tied up in food chains or webs, how will these structures change dynamically? What new phenomena play a role at the population as opposed to the individual level?

Except for work in the tradition of mathematical demography on which modern age-structured population dynamic theory is based [157], most publications on population dynamics, up to some years ago, have dealt with unstructured populations, i.e. populations that can be characterized by the number of individuals only. So all individuals are treated as identical, and are merely counted. This also applies to microbiology publications, which basically deal with microbial populations and not with individual cells. This has always struck me as most unrealistic, because individuals have to develop before they can produce offspring. The impact of a neonate on food supplies is very different from that of an adult. In the chapter on population dynamics, {326}, I show that neonates producing neonates

themselves can dominate the dynamics of unstructured populations. This absurdity makes one wonder to what extent unstructured population models have something useful to say about real populations. Many modern views in ecology, e.g. concerning the relationship between stability and diversity, are based on models of unstructured populations.

I will use arguments from energetics to structure populations, i.e. to distinguish between different individuals. This, however, complicates population dynamics considerably, and the first question to be addressed is: does this increase in complexity balance the gain in realism? I know only one route to an answer: try it and see!

1.2 The art of modelling

1.2.1 Strategies

Before I start to develop a theory for energetics, I think it is important to explain my ideas about theories and models in general. It is certainly possible that you may disagree with part of what follows, and it is helpful to know exactly where the disagreement lies. The source of a disagreement is frequently at a point other than where it first becomes apparent. The final chapter, see {357}, evaluates the DEB theory in the light of the points of view presented in this section. I started this chapter by pointing to growth curves as an example, because they feed the hope that it is possible to build a quantitative theory that is not species-specific. My primary interest, however, is not limited to growth curves, it is far more encompassing. How do phenomena operating at different levels of organization relate to each other and how can these relationships be used to cross-fertilize different biological specializations?

Let me state first that I do not believe in the existence of objective science. The types of questions we pose and the types of observations we make bear witness to our preconceptions. There is no way to get rid of them. There is nothing wrong with this, but we should be aware of it. When we look around us we actually see mirrors of our ideas. We can try to change ourselves on the basis of what we see, but we cannot do without the projections we impose on reality. Observations and statements span the full range from facts via interpretation to abstract ideas. The more abstract the idea, the more important the mirror effect. Let me give an example of something that is not very abstract. I spend a long day looking for a particular plant species. At the end of the day luck strikes, and I find a specimen. Then I return home, using the same path, and shame, oh shame, this species turns out to be quite abundant. To make matters worse, I am quite experienced in this type of activity. So, if someone maintains that they would not miss the plants, I am inclined to think that they are simply not able to criticize their own methodology.

I do not believe in the existence of one truth, one reality. If such a 'truth' did exist, it would have so many partially overlapping aspects, that it would be impossible to grasp them all simultaneously and recognize that there is just one truth. A consequence of this point of view is that I do not accept a classification of theories into 'true' and 'false' ones. In connection with this, I regard the traditional concepts of verification and falsification as applied to theories as meaningless. Theories are always idealizations, so, when we

look hard, it must be possible to detect differences between theory-based predictions and observations. Therefore, I have taught myself to live happily with the knowledge that, if there were only one reality and if theories can only be classified into ‘true’ or ‘false’ ones, all of them would be classified as ‘false’. As it is not possible to have the concept ‘a bit true’, believers in one reality do not seem very practical to me. Perhaps you judge this as cynical, but I do not see myself as a cynic. Discussions suggest that colleagues with a quantitative interest are more likely to share this point of view than those with a qualitative interest.

Instead of designating theories as ‘true’ or ‘false’, I classify them on the basis of their usefulness. This classification is sensitive to the specification of a purpose and to a ‘state of the art’. Theories can be most useful to detect relationships between variables, but can lose their usefulness when the state of the art develops. Theories can be useful for one purpose, but totally useless for another. When theories produce predictions that deviate strongly from observations, they are likely to be classified as useless, so I do not think that this pragmatism poses a threat to science in the eyes of the apostles of K. R. Popper. Although it is satisfying to have no difference between prediction and observation, small differences do not necessarily make a theory useless. It all depends on the amount of difference and on the purpose one has in mind. A ‘realistic’ description then just means that observations and descriptions do not differ much. There will always be the possibility that a well fitting description rests on arguments that prove not to be realistic in the end. Perhaps you think that this is trivial, but I do not. Take for instance goodness of fit tests in statistics, where the null hypothesis is held to be true, and how they are applied, e.g. in ecological journals. The outcome of the test itself is not instructive, for the reasons given. It would be instructive, however, to have a measure of the difference between prediction and observation that allows one to judge the usefulness of the theory. Such measures should, therefore, depend on the theory and the purposes one has; it would be a coincidence to find them in a general text on statistics.

The sequence, ‘idea, hypothesis, theory, law’ is commonly thought to reflect an increasing degree of reliability. I grant that some ideas have been tested more extensively than others and may be, therefore, more valuable for further developments. Since I deny the existence of a totally reliable proposition, because I do not accept the concept of truth, I only use this sequence to reflect an increasing degree of usefulness. It is, however, hard and probably impossible to quantify this on an absolute scale, so I treat the terms in this sequence more or less as synonyms. Each idea should be judged separately on its merits.

Mathematics as a language is most useful for formulating quantitative relationships. Therefore, quantitative theories usually take the form of mathematical models. This does not imply that all models are theories. It all depends on the ideas behind the model. Ideally a model results, mathematically, from a list of assumptions. So, I am inclined to identify sets of assumptions with theories. The formulation of empirical models does not start with mechanistically inspired assumptions, and directly aims at models that describe data sets. Although useful for certain applications, such models have little to do with theories.

When model predictions agree with observations in a test, this supports the assumptions, i.e. it gives no reason to change them and it gives reason to use them for the time being. As explained on {14}, the amount of support such a test gives is highly sensitive